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With the author's respects

THEORIES OF EVOLUTION SINCE DARWIN

BY

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It was no coincidence that the two men who independently arrived at the theory of evolution through natural selection were, in the highest sense, field-naturalists who had won wide acquaintance with the objective side of nature, for the chief merits of the theory, and probably its most enduring features, are due to its foundation upon actualities of organic life so universal that they are not to be denied.

From overproduction of offspring, from the existence of variation, and from the extinction of individuals not fitted to contend with the destructive forces surrounding them from the moment of their birth, Darwin and Wallace derived the law of survival of those whose variations of structure enable them to succeed and so to become the parent stock of the next generation—a process to which Darwin gave the name, not altogether well chosen, of Natural Selection. Before an audience such as this no detailed account of Darwinism can be required, and it is enough to point out that within the period of half a generation after it was given to the world it had gained almost general acceptance among biologists as a probable statement of the method of evolution. Yet certain difficulties remained whose gravity in the light of the knowledge of that day was admitted by Darwin himself. Chief among these appeared to be the explanation (1) of how the minute variations in the direction of new organs, which were all that were then believed to occur, could have so determining a relation to survival as to permit the action of natural selection, and (2) why, taking place as was then believed, in one, or at most in a very

few individuals only, they are not immediately lost, or "swamped," as the usual term has it, in the normal average state of the species, maintained by free interbreeding. I shall return to these difficulties in considering the efforts which have been made to resolve them.

Before its author's death Darwinism became something quite other than he had made it, as a result of the views put forward by August Weismann.

It is not necessary to the present purpose, nor am I competent, to review the whole of Weismannism, the greater part of which was devised in completing his scheme of heredity, which by a logical necessity became a system of evolution as well—or, more exactly, was found to profoundly modify all previous theories of like nature.

Weismann postulated as the machinery of inheritance an unalterable substance, called by him "Germ Plasm," conveying every characteristic of a species and handed down from individual parent to individual offspring, and so closed off from the possibility of being acted upon either by conditions external to the individual, or from being modified by changes in the body which was its host, that it could vary only from an admixture, in an act of generation, with the germ plasm of another strain.

Most obviously, if such were the case, the inheritance of acquired characters and the Lamarckian factors are disproved, and the sole agency concerned in evolution has been the action of natural selection, resulting in the preservation and accumulation of small congenital variations determined wholly from within. From this conclusion the inference was drawn by Wallace and others that utility has necessarily been the universal and only principle concerned in the development and preservation of species, and that every organ and every structure in plants and animals, to quote Wallace's words, "must now be or once have been *useful* to the individuals or the races which possess them."

Now it is not to be denied that this deduction is logically correct if the premise upon which it is based is cer-

tain, but that is so far from being the case that Weismann himself does not now hold it as true in its strict original form, although Wallace still maintains the validity of his law of utility. It is to be observed concerning Weismannism that it is itself little more than a logical system erected with great ingenuity upon a basis consisting of certain observed facts in embryology and a greater number of assumptions, either unverified or unverifiable. It has, furthermore, so failed to satisfy even its author that he has modified the original theory by the vital admission that at times, under conditions quite unknown, germ plasm may be influenced by long-continued external causes in such manner as to affect the inheritance of the race. The influence wrought by Weismann upon evolutionary thought is chiefly this: that while the dogmatic assertion that natural selection is the sole cause of evolution is confined to Neo-Darwinians, as his strictest followers are termed, the exclusive valuation given to the principle has brought prominently under discussion the two elementary difficulties which I have mentioned, and has furthermore brought about renewed inquiry into the inheritance of acquired characters. Discussion of the last question was greatly promoted by the growth of the Neo-Lamarckians, almost concurrently in time with the development of Neo-Darwinism. This school, chiefly of American zoölogists headed by Cope, Hyatt, Packard, and Ryder, found the explanation of evolution mainly in use and disuse and in the direct responses of the organism to the stimulus of external conditions, developing in adaptation to them alterations of structure, to be inherited and improved upon by its descendants. They were less narrow, however, than their opponents, for they did not claim exclusiveness for their principle, but admitted the agency of natural selection as well.

It is clearly seen that their main principle stands or falls with use-inheritance, but its weakness lies in the fact that, however pleasing to the imagination, and notwithstanding the many problems that would find ready

explanation if it were true, use-inheritance is as far from being experimentally proved to-day as it was in Lamarck's own time.

As schemes of evolution Neo-Darwinism has largely, and Neo-Lamarckism almost wholly, lost direct influence upon the younger biologists of to-day, however much they have combined to direct them into new paths of observation and experiment.

Of altogether later influence in evolutionary speculation is the belief which has taken hold of many palæontologists that evolution, instead of being haphazard and resulting in lines determined only by extinction of intermediate forms, has been in determinate directions. It should be observed that determinate evolution may be a very different thing from determinate variation, and requires for its fulfilment no necessary law of progress inherent in the organism itself. While this is true, there are palæontologists who hold the opinion that variation has also been determinate, but the evidence for this cannot yet be held as conclusive.

The main questions then, which at this point natural selection unaided is not regarded as fully competent to explain, are (1) the small beginnings of organs, (2) the certainty that chance individual variations would promptly disappear under free interbreeding of all the members of a species, and (3) determinate evolution.

Let us look at the supplementary theories by which it is sought to explain these problems:—

The statistical method of study has shown that variation is much greater in extent and more frequent in occurrence than was known to be the case in Darwin's time. Its range frequently amounts to as much as twenty-five per cent. of the average of a structure, and its occurrence is distributed according to the mathematical laws of chance around that average. So that in each species at any given time there are large numbers of individuals presenting a given character, or organ, just above or below the mean, and a rapidly diminishing number

toward the extremes. If then, through stress of hardship it should become of advantage that such organ should be increased or diminished, material will be at hand offering variations of some magnitude and in considerable numbers in the indicated direction. Natural selection, therefore, does not have to act upon rare and single instances, but upon considerable groups, and by the extinction of those failing to reach the lowest standard possible for survival, the whole average of those remaining of the species is raised. It has, however, also been found that variation of this kind is rarely more than quantitive, it is only in degree, for which reason it appears that advance by means of their selection must be in the main limited to the direct line of advance or retreat, through the averages maintained by free interbreeding. If this view is correct, continuous evolution of a species as a whole is accounted for, but the method does not provide for the protection from interbreeding of the variations diverging from the general line, through the preservation of which the original stock may be split into two or more species. Another difficulty, therefore, to be explained is how divergent evolution is to be accounted for. So, on the whole, while the question of the ability of natural selection to take hold of minute initial variations is made more easy, and that of their being lost through interbreeding is lessened, determinate evolution and divergence of character remain unexplained without the aid of other causes.

To satisfy the needs of interbreeding and divergence the highest measure of efficiency was accorded by the late Dr. Romanes to the principle of *Isolation,* the need for which he demonstrated with the wealth of keen reasoning so characteristic of his brilliant essays. Later he was followed by the Rev. Mr. Gulick, who brought to the aid of Romanes' theoretical considerations a great number of facts observed by him while engaged in collecting the land shells of the Hawaiian Islands. Few theories have had more able support than was given to the one now in question by these two naturalists.

Common use of the word isolation rather conveys the notion of separateness in space, and chiefly in this sense, as geographical isolation, it was recognized as of subordinate importance by Darwin, especially in his later years, but a far broader significance is now given to it, and there can no longer be question that its influence in the development of species has been very great—indeed, without its concurrent existence, it must be gravely questioned whether natural selection can answer for divergent evolution. Isolation, in the sense of Romanes and Gulick, includes every condition, physiological or physical, internal to the organism or pressed upon it by the nature of its surroundings, which results in the establishing of a bar to free breeding between any number of the individuals of a species and the rest of its members. Stress is laid, especially by Romanes, upon the probability that even the early stages of divergence of character are accompanied by the beginnings of infertility between the diverging stock and the main stem of the species, thus enabling the variants to escape the leveling effects of free breeding. He even believes that variation in degrees of fertility alone may lead to isolation and divergence. This principle he calls *Physiological Selection.*

Other forms of isolation are geographical separation; differences in station resulting from change of habit or kind of food; alteration in the reproductive season; and perhaps sexual selection resulting in preference. By these means the varying section is enabled to breed within its own limits and carry on its own line of development.

That isolation must be a powerful agency in divergence of character is certain, both on grounds of logic and from observation, but like many other children of human thought it is viewed somewhat out of perspective by its authors. Indeed, they go so far as to speak of natural selection as only a form of isolation, in which they really commit an ambiguity, for they are using their term as equivalent to the whole of evolution. A species is such by reason of its isolation from other species, and it is only when taken in that sense that natural selection can be

viewed as subordinate to it. Isolation, indeed, is not a principle but a condition—less an agency than a result, and Mr. Gulick's term *Segregation,* intended to be synonymous with it, might better be limited to denote the processes which lead to it. Isolation being regarded as an essential condition to the existence of species, in my opinion the most important contribution which has been made to our understanding of segregation as a process, is its division by Gulick into two classes: *discriminate,* in which the separated portion differs from the remainder in the common possession by its members of one or more identical peculiarities which become the starting point of a new species; and *indiscriminate,* in which the portions are separated by migration, or any cause which does not select those of like variations. It is perfectly clear that discriminate segregation must lead to divergent evolution, for the portions of a species so segregated differ from the beginning; but it has in addition been cleverly pointed out by Gulick that indiscriminate segregation will also result in divergence, for if a species be subjected to mere numerical division into a larger and a smaller portion, it is mathematically certain that the average character of the two groups will be slightly different, and as evolution advances by averages, each successive generation should widen the initial difference in the two stocks.

It is important to notice that segregation does not, like natural selection, require extinction of the nearest competing groups. In most cases the difference in range, station or habits will much lessen the struggle between varieties while forming—the intra-specific struggle—while that with more remote or unrelated species remains. When physiological selection is the only cause of segregation, natural selection may still determine the extinction or survival of one of the segregated groups. It is by no means clear, however, that physiological selection alone can produce the results claimed for it by Gulick and Romanes, for even if it were possible to suppose that individuals fertile with each other but infertile with all others, were scattered promiscuously through the species, there would be little chance of their mating together,

while if these mutually fertile individuals were grouped together at the start, it could be owing only to some other cause of segregation. I should point out again that isolation, like survival, is not a mere product of logical thought, but is a fact in nature. Natural selection is chiefly concerned in survival, but other causes may lead to isolation.

Prominence has been given in recent years to the *Mutation Theory* of deVries, to a greater extent than seems justified by an examination of its terms and of the experiments upon which it is based. The term "mutation" is by no means well chosen, for Waagen had already applied it to the progressive changes shown by palæontology, taking place in structure in succeeding geological periods, such changes as those which Osborn now calls "definite variation." These changes are widely different from the discontinuous variations of deVries, and he would have done better to label his theory with the name "saltations," used by St. Hilaire to express very similar views.

The question of "sports" was given full consideration by Darwin, with the conclusion that they have not played much part in the formation of species, and sports, which are variations in excess of or outside of the normal range, are mutations in the sense of deVries, or, at least, no valid reason has been shown for believing them to be otherwise. The questions concerning their influence in evolution are three: (1) do they differ in kind from varations in the Darwinian sense? (2) are they of frequent occurrence? and (3) are they inherited? There is excellent reason to doubt the conclusion of the Dutch botanist, who answers all three in the affirmative, and asserts that they have been the sole starting point of new species, and that the natural selection of slight variations has given rise to nothing more than more or less unstable varieties within narrow limits.

Now the fundamentally unsatisfying part of the system constructed by deVries is that it is built upon mutations occurring and perpetuated in garden varieties of plants cultivated with the most minute care and attention in his garden at Amsterdam. These garden varieties, as a rule, are the result of mixing together by the horticulturist of a number

of distinct strains, or even varieties. The plant from which deVries in his own opinion got the best results, *Œnothera lamarckiana,* one of the evening primroses, seems to be known only as a garden variety of unknown pedigree. Its origin is so far in doubt that it is not certain whether it is European or American, and absolutely nothing has been learned of the early history of the stock from which came the plants experimented upon by deVries. This is not the kind of material best suited for exact investigation of the problems of variation and inheritance, and while it is true that deVries draws a distinction in kind between his "mutations" and mere reversions, it is to be observed that this is no more than an opinion as yet unjustified by experimental proof.

In the two remaining plants from which mutations were obtained, the peloric toad flax and the corn marigold, it is curious to observe from deVries' own narrative, that the most extreme and careful selection was practised by him on numerous generations in each case, even to the rigorous destruction of every plant except those selected for breeding, before the mutations appeared, and that these were then kept up under absolutely uniform conditions, supplemented by close breeding. Now the analogy between artificial and natural evolution is by no means perfect enough to bridge the gap from controlled lines of experiment such as these, to the actual course of nature, and the assumption that the process is alike in both cases must be regarded as highly speculative.

The securing of evidence to support this theory from what actually does take place under nature is obviously difficult almost to impossibility, for a mutation having once appeared in a wild state, in most cases there would be no way for the botanist to tell with certainty whether it had sprung, like Venus, full grown into existence, or whether it had a history of progressive development. One of the essential steps in deVries' theory of evolution is the definition of his categories of the constituent parts of species: *elementary species*— his units of evolution—and *degressive* and *regressive varieties.* However interesting these may be as the concep-

tions of a clever mind concerning species and varieties, there seems to be no valid reason why they should be looked upon as anything more than formal definitions, of doubtful value to the biologist in theory and no value at all to the systematist in practice, especially if he be a zoölogist, for their recognition in most cases would require a knowledge of the race history for many generations, which is rarely available. The hard-and-fast proposition that varieties differ from each other only in one or two characters, while species differ in all, or nearly all, is too arbitrary as a distinction of taxonomic values to meet with much acceptance.

To the best of my knowledge no great amount of investigation has yet been conducted by zoölogists into the field of mutations. The elaborate work of Bateson hardly goes beyond the collection of cases, mostly of quantitative variation, which, if serviceable at all in evolution, would be mainly limited to linear advance or retreat, but for the most part they seem to belong to deVries' classes of degressive or regressive varieties, which in the opinion of that author have not contributed to the establishing of new species. No reason, furthermore, has been shown by Bateson or deVries why these discontinuous variations, confessedly occurring in rare or single instances, should be free from the law of disappearance under free breeding which is so generally admitted in the case of lesser variations. It is clear that experimental study in anything above the lower groups of animals is most difficult, owing to the length of the time required between the breeding periods of successive generations high in the scale, and to the almost invariable presence of some degree of sterility in species of vertebrates when rendered captive.

In so far as its occurrence under nature is concerned, every zoölogist who has worked over many genera for purposes of taxonomy will probably admit that many of his most perplexing anomalies, which occur now and then as one or a few individuals which cannot be exactly placed, are in the nature of mutations, but few, I imagine, will be disposed to allow that they find evidence that these are inherited. Notwithstanding its exalted claim, and the fact that there

appears to be no logical difficulty involved in its terms, it appears to me that the mutation theory has advanced the importance of "sports" but little beyond where they were left by Darwin, except that in estimating their value as factors of evolution, we may now speak of them as probable, rather than possible, but there is little evidence that they have been frequent starting points of new species. In no case would the magnitude of the departure presented by them relieve them from the trial by natural selection.

The one main theory left for mention contains more of originality than any other brought forward since Darwin's death. Indeed it may be said to be wholly original and to comprehend the only factor of evolution under serious discussion in these days which was not, in some phase at least, considered by Darwin himself, and in that respect is the more remarkable in that it was developed independently by three men: Osborn, of New York, Baldwin, of Princeton, and Lloyd Morgan, of England. I speak of the theory of *Organic Selection,* which professes (1) to fix the place in evolution of adaptive structures without requiring use-inheritance, (2) to show how natural selection can take hold of slight congenital variations and (3) to account for determinate lines of evolution.

Organic Selection recognizes that adaptive changes are acquired by individuals in response to altered habits and to changes in surrounding conditions, but admits the doubt that they are transmitted to offspring. These *ontogenetic modifications,* as they have been termed, die with each generation, to be gained anew in the next, and so far are without direct influence on the race. What, then, is their function in evolution? Simply that they afford the means by which the more plastic members of a species adapt themselves to new habits, or survive under the stress of new conditions, and keep the species in existence until congenital variations occur of a kind useful in the new habit or under the new conditions, when these will be seized upon by natural selection and preserved to become the inheritance of succeeding generations.

This theory is not altogether easy to grasp, and a crude illustration may perhaps serve to render it clearer. If it be

supposed that a group of monkeys living chiefly upon the ground are forced by physical changes in the region they inhabit, or by the introduction of a new terrestrial enemy, to take to a life in trees, it needs no argument to show that the survivors who will perpetuate the species will be those individuals who adapt themselves to the new needs, perhaps those whose fingers and toes readily acquire the habit of firm and certain grasp, or whose flexor muscles become strengthened and supple under the new use, or who more quickly establish the complex coördinations required in an arboreal life. These new aptitudes are not handed on to the offspring must be gained anew in each generation, but obviously if they are so gained, they would keep the species alive as long as the conditions continue to which they are adapted. Sooner or later congenital variations will surely appear, perhaps of such nature as increased length of fingers and toes, or even of quite different kind from the acquired modifications, such as a more oblique articulation of the lower leg bones on the tarsus, or in the direction of a prehensile tail. Each one of these variations, being in the direct line of use to a tree-living species, would contribute its share from the very beginning to survival and be taken hold of by natural selection, to follow a course of progressive development. The acquired modification simply gives time in the life-history of the species for the occurrence of suitable chance variations. Organic selection would account for the fact that evolution has apparently followed definite lines to a determinate result, by pointing out that the ontogenetic modifications determine the survival of a species as long as it follows a particular course under fixed and continuing conditions, and as long as these remain the same, or nearly so, the congenital variations selected will be those only which are of use in the existing mode of life. The species will therefore advance in the direction indicated by its own choice, or by its physical environment, until this is again greatly changed, when it will take up with new modifications and survive, or fail to adapt itself and perish. Organic selection requires both natural selection and isolation, indeed it leads to isolation, and as a logical system it has been

approved by leaders among Neo-Darwinians such as Weismann and Wallace; but its experimental proof is not easily forthcoming, for the obvious reason that there is no uniform measure to determine which are ontogenetic modifications, or which congenital variations, except at the time of birth, and in wild species such an opportunity can rarely occur. But granting that adaptations occur and that they may be of life-saving value—and no biologist will deny either proposition—it must be admitted that without inheritance it is highly probable that an indefinite number of succeeding generations might acquire them with much uniformity, their growth being greatly aided by example and imitation—by tradition, to use a psychological term. In some cases they may persist with the development of new inheritable organs by natural selection, but usually they would in time be supplanted by them.

It is to be observed that a consequence of some importance to our formal conception of a species follows from bringing ontogenetic modifications so prominently to the front, for the characters so originating are not specific in the usual, older sense of being inheritable, and species distinguished by them being wholly subject to the environment are of like transient nature as the groups we are accustomed to call local races, or climatic varieties, and as we have seen already, we are not in most cases able to distinguish between such species and those owing their distinctive characters to a congenital origin. As we can see no way to discriminate between these two kinds of characters, the somatogenic and the blastogenic, a conception of species for use in taxonomy must comprehend both. If, therefore, these modifications do follow by individual adaptation in each generation to the extent supposed by organic selection, the feature of inheritance must be left out of our definition of what constitutes a species. This change, however, is of more logical than practical significance, since in real use the systematist does not, as a rule, consider the question of inheritance.

Another modifying influence upon present methods of classification appears in the facts of parallel and conver-

gent evolution, of which palæontology has been accumulating evidence. If like conditions of life tend to induce similar modifications in unrelated groups, it at once becomes evident that a system of classification based upon such likenesses of structure may not in all cases reflect the genetic connection which, since Darwin, we have believed them to approach. Classification in the modern sense is worthless if it fails to correspond to descent. It seems not unlikely, therefore, that geographical considerations may come to enter more largely into the composition of genera than has heretofore been the rule with conservative naturalists, for in a strictly genetic system it would not be admissible to place in the same genus species so widely separated by present and past geographical barriers, that we are forced to believe that they can not have developed from a common source.

It has been doubtless observed that several contributions to post-Darwinian speculation have been passed without notice—notably Weismann's theory of Germinal Selection, and such verbal mysteries as "bathmisms," or Naegeli's "perfecting principle." With logical systems built upon no basis more substantial than words the methods of science have no serious concern. Whether they be wholly or partly true or false there is no means of determining, and they are as barren of results as the metaphysics of two centuries ago.

Just as in species there is a mean of characters around which the variations range, so there is always an average in human thought, and it may now be asked, what is the present mean of biological opinion concerning the factors of evolution? The answer is not easily found, for the fluctuations are many and in some cases almost extreme enough to be called mutations.

The following conclusions perhaps represent in a measure such an average:—

(1.) It would seem, on the whole, that the present time exhibits a return to the position occupied by Darwin, in so far as he always admitted that other factors besides

natural selection had been concerned in evolution. In his own simple words, "I am convinced that natural selection has been the most important, but not the exclusive means of modification."

(2.) With regard to variation, there seems more and more reason to believe that it, quite as much as inheritance, is an elementary property of organic life, and that inquiry into its origin is in great part an inquiry into the ultimate nature of living matter, but its results in structural characters are more sharply divided than formerly into those congenital and those acquired.

(3.) How far congenital variation may be induced by external influences acting upon the individual body is yet under judgment, except by the extreme disciples of Weismann, for the inheritance of acquired characters awaits experimental proof and is more than ever held in doubt.

(4.) Natural selection remains the means by which the survivors of a species are determined in time of hardship, but it has come to be recognized as most probable that congenital endowments only emerged from its action as the inheritable portion of the superiority of the survivors.

(5.) It is reasonably clear that natural selection acting by itself can result only in linear, or monotypic evolution, and that isolation must be established to account for divergence, as well as for the fact that variations do not in all cases disappear through free breeding, the tendency of which is always to maintain the average stability of the species.

(6.) Whatever may be the thought of botanists, among zoölogists no cordial acceptance of evolution exclusively *per saltum*, as required by the mutation theory, has yet appeared.

(7.) Organic selection rests upon so sound a basis of logic that the actuality of its occurrence can hardly be doubted, but there has not yet been time to reach conclusions as to how much or little it may have facilitated the action of natural selection, and the breadth of its range is yet undetermined. It seems clear that the botanist must hold it less serviceable than the zoölogist.

(8.) Determinate variation is yet a doubtful hypothesis, but determinate evolution, while still below the mean of biological acceptance, is held by most palæontologists, who more than others meet directly with its evidence. But its explanation is sought, not in teleological contrivances, nor in innate tendencies to progress, but in the reactions of the organism to the condition of the environment in which it finds its place, the special path which it is to follow being determined partly by conscious but chiefly by unconscious aptitudes and adaptations by which its plastic material responds to outer stress.